The composition and spatial organisation of mixed-species flocks in a Sri Lankan rainforest

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We made a total of 476 observations on the composition and spatial organisation of flocks in lowland to mid-elevation rainforest in Sinharaja World Heritage Reserve, Sri Lanka, during 1981–1984 and 1995–1998. Flocks contained 10.9 species and 41.3 individuals on average. The composition of flocks was generally stable over time, changing little over the annual cycle or between the 1980s and the 1990s, although the abundance of some species appears to have changed following regeneration after logging in the 1970s. Flocks were larger, more diverse, and had a different composition (including more endemic and threatened species) compared to those described from the montane zone of Sri Lanka. They were typical of near-equatorial mixed-species flocks in that they included few migrants and were generally dominated by insectivores. They were unusual, however, in the numerical dominance of a single species, Orange-billed Babbler *Turdoides rufescens*, which averaged more than 16 individuals per flock and which was found in c.90% of flocks. This species and Greater Racket-tailed Drongo *Dicrurus paradiseus* are both possible 'nuclear species' for these mixed-species flocks, providing foraging and/or anti-predation benefits to other flocking species.

INTRODUCTION

Mixed-species flocks are a prominent form of social organisation of foraging birds, particularly in the tropics (Powell 1985). In general, the occurrence of such flocks has been explained in terms of adaptations to reduce predation and increase foraging efficiency (reviewed in Morse 1977, Terborgh 1990). Flock systems vary widely in the numbers of species and individuals involved, with some of this variation explained by factors related to predation, including the openness of the vegetation and the density of avian predators (Thiollay 1999). More studies from different regions and habitats in the world are needed to further document the diversity of flock systems and better understand the applicability of the hypotheses that explain flocking.

In Sri Lanka, mixed-species flocks have been studied in the montane region (Partridge and Ashcroft 1976). A distinct and more diverse system, however, can be observed in the low to mid-elevation rainforests of the wet south-west part of the country, where avian diversity and endemism are higher. Here the flock system centres around the endemic, highly gregarious Orange-billed Babbler *Turdoides rufescens*. Several authors have commented on the tendency of babblers Timaliini to lead mixed-species flocks in the Indian subcontinent (Ali and Ripley 1987, Grimmett *et al.* 1999). Such flock systems have yet to be described systematically, although some of the flocks described by King and Rappole (2001a) in Myanmar were characterised by a very high number of laughing-thrushes.

Here we describe mixed-species bird flocks in Sinharaja World Heritage Reserve, one of the largest rainforest tracts remaining in Sri Lanka, focusing on their composition and spatial organisation. We first took observations on flocks during the early 1980s, following logging in the reserve during the 1970s, and we then repeated the observations in the late 1990s. Our original objective was to use flocks as an indicator of how the avifauna had changed over this fifteen-year period of forest regeneration. Intrigued by the phenomenon of mixed-species flocking, however, we expanded our aims to include (a) comparing the size and composition of the Sinharaja flocks to those described from the montane zone of Sri Lanka, and from other parts of the forested tropics, and (b) investigating the benefits that birds accrue in flocks and identifying which species are most essential to flock structure. In pursuit of this latter objective, we investigated how closely species foraged together in flocks, focusing on the relationship between the Orange-billed Babbler and other species. Such information is important because proximity is relevant in assessing whether species gain foraging benefits from associating with other flock members (Hutto 1994). We also collected information on which species lead flocks, as this is a principal characteristic of 'nuclear species', those that are important for the formation and/or maintenance of mixed-species flocks (Moynihan 1962, Hutto 1994).

STUDY SITE

The study was conducted in the north-western sector of Sinharaja World Heritage Reserve, Sri Lanka (6°26′N 80°21′E, 450–600 m). The vegetation consists of dense, evergreen rainforest, dominated by *Mesua* spp. and *Shorea* spp. trees in the canopy (Gunatilleke and Gunatilleke 1981). Annual rainfall averages c.4 m with distinct dry (January–March) and wet seasons (April–December); diurnal temperatures range from 20°C to 25°C (Gunatilleke and Gunatilleke 1981).

The north-western sector of the reserve was logged in the 1970s (De Zoysa and Raheem 1987). The effects of the logging in the reserve were heterogeneous, so that some areas on steep ridges were completely uncut, whereas gaps were created near the logging roads. During the 1980s, we walked a network of logging roads near the Sinharaja Research Centre, formerly the centre of the logging operation, looking for flocks. By the 1990s most of these roads were overgrown, with the exception of a 3.5 km stretch that led from the entrance of the reserve, past the Research Centre, towards the Sinhagala lookout.

METHODS

Flock composition and size

Data were collected in five different surveys by different observers: SWK and P. B. Karunaratne in 1981–1982, C. R. Thambiah in 1983–1984, EG in 1995 and 1997–1998, and EG and R. A. R. Perera in 1996. Data are stored in the March for Conservation and the Field Ornithology Group of Sri Lanka archives, University of Colombo. In total, we made 219 observations of flocks in the 1980s and 257 in the 1990s. While the 1980s surveys were year-round, the 1995 and 1996 surveys were confined to June–August. In order to compare between the decades, we made at least 10 observations of flocks per month between September and May in 1997–1998.

In all surveys we used the same methodology. Flocks, defined as two or more species moving in the same direction, were observed throughout the daylight hours, covering the stretch of roads evenly. When a flock was encountered, the observer would stay with the flock until he concluded that all species had been recorded. The number of individuals of each species was recorded as the highest number of birds seen at one time or during one crossing of the road or path. We were frequently unable, however, to count the number of individuals of the most abundant species, and thus only 298 of the total 476 records had complete information on the total number of individuals in the flock. To minimise repeated observations of the same flocks, we took data from only one flock per 250 m stretch of road per day. However, some pseudoreplication is likely to have occurred because the same individuals were undoubtedly resampled on multiple days (see below).

During the 1996 and 1997–1998 survey, we used the 3.5 km stretch of logging road as a transect, recording all individuals of species and noting whether they were in flocks or outside of them. From these data we calculated each species propensity to flock, defined as the percentage of all individuals of the species recorded that were seen in flocks (Thiollay and Jullien 1998).

Foraging in flocks

We collected information on diet and foraging technique from a literature search (Legge 1880, Phillips 1935, Henry 1971, Ali and Ripley 1987, Grimmett *et al.* 1999) and from field observations. We characterised species by their major food sources, as insectivores, omnivores and frugivores. Separate foraging observations (n=673), primarily on insectivorous birds, were made in February–March 1998, in closed-canopy forest. Focal individuals were selected randomly, with one record taken per species per flock, except when more than one individual could be seen simultaneously; we avoided taking repeated observations of flocks within the same stretch of road. We categorised insectivorous foraging techniques as hawking, hovering, gleaning, probing, tapping, and scratching on the ground (Eguchi *et al.* 1993). We analysed only those species with more than 15 observations.

Spatial organisation in flocks

We recorded the order in which birds crossed the road during the 1990s surveys, for a total of 83 road crossings. We summarise this information by giving each individual bird a crossing score, defined as the position of the bird in the crossing (first, second, third etc.), divided by the total number of birds that crossed. While taking foraging observations we also recorded the foraging height of the focal individual, the species identity of its nearest neighbour (Hutto 1994), and the distance to the nearest Orange-billed Babbler.

Statistical analysis

The sampling method of repeatedly walking the same road circuit raises questions about the independence of the records. Flocks in Sinharaja show some characteristics of having home ranges, as there are distinguishable 'hotspots' of flock activity (we noted nine such areas on the 3.5 km stretch of road that were stable over several years; flocks could be seen at adjacent hotspots simultaneously, and these hotspots therefore probably represent nine different sets of birds). However, flocks are also highly dynamic with some characteristics of waves, as individuals join flocks and then fall out, and flocks merge together and break apart. In this analysis, we treat all observations equally, because we found no evidence that the location of the flock predicted its composition: when we subjected flocks to a cluster analysis based on the presence and absence of species, we found flock records from the same hotspot to be spread through the dendrogram.

We used single-classification ANOVA models to determine whether flock size changed over time, whether there was a relationship between species' diet and their flocking propensity, how species differed in their horizontal and vertical positions in flocks, and in their distance to a babbler. *Post-hoc* multiple comparisons were done using the Tukey HSD approach, or the Gabriel method when sample sizes were considerably unequal (Sokal and Rohlf 1995). In the analysis of species' frequency over time, we analysed 30 species found in at least 10% of flocks. In the analysis of the relationship between diet and flocking propensity, we included 35 species that were seen, inside or outside of flocks, in at least 20 observations. We arc-sine transformed the propensity variable to improve normality (Sokal and Rohlf 1995). We analysed two-way tables to determine whether species changed in their frequency in flocks over time, and whether species varied in their tendency to lead flocks or to be close to babblers. All analysis of proportions was done using G-tests with Williams's correction; we reduced the significance level by the Dunn-Šidák method when making multiple tests (Sokal and Rohlf 1995). Sample sizes are presented ± 1 standard deviation.

RESULTS

Flock composition and size

Flocks averaged 10.9 (±4.5, n=476) species, with 59 bird and five mammal species seen in flocks. By far the most frequent flock members were Orange-billed Babbler and Greater Racket-tailed Drongo *Dicrurus paradiseus*, each of which was present in c.90% of

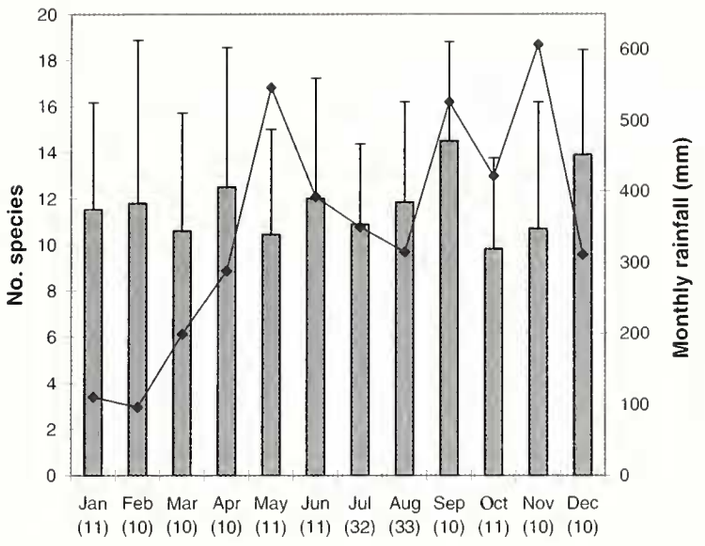

Figure 1. Flock size (bars) did not vary widely seasonally, although the monthly rainfall (line) varied five-fold. Flock size data comes from the 1990s surveys; rainfall data is for the months in which the survey took place, and comes from Kudava, 5 km from the Sinharaja Research Station (courtesy the Sri Lanka Department of Meteorology). Number of flock observations each month is shown in parentheses.

flocks. Nineteen other species were involved in more than 25% of flocks, qualifying as 'regular members' (Powell 1985;Table 1). Mammals (dusky palm squirrel *Funambulus sublineatus*, Layard's palm squirrel *Funambulus layardi*, Indian palm squirrel *Funambulus palmarum*, grizzled giant squirrel *Ratufa macroura*, and purple-faced leaf monkey *Trachypithecus vetulus*) were rare in flocks, although the three *Funambulus* spp. squirrels collectively occurred in 25% of flocks. These small squirrels appeared to be as much members of the flocks as the birds, repeatedly moving in the same direction as the flock.

Flocks averaged 41.3 (±22.9, n=298) individuals. Although the majority of species were represented by 1–3 individuals per flock (Table 1), Orange-billed Babbler averaged 16.2 (±10.8; n=268) individuals per flock, with occasionally more than 50 individuals. When this species was present in flocks, 37% of the individuals were Orange-billed Babblers. Furthermore, at any moment in time, Orange-billed Babblers were an even larger proportion of the flock than this, since they stayed with the flock continuously whereas other species joined and then left flocks (even if a species moved with the flock only once it was counted as a flock member).

Changes in flock composition and size over time

Flocks showed a large degree of consistency in size and composition between the surveys of the 1980s and the 1990s. The number of species increased significantly, although not dramatically, over the time interval (1980s: mean=9.9±4.3, n=219; 1990s: 11.7±4.6, n=257; t_{474}=4.16, P<0.0001). There was no significant change in the number of individuals during the period (1980s: mean=40.7±24.3, n=129; 1990s: 42.4±21.9, n=169; t_{296}=0.66, P>0.50). Composition was also largely stable over the period (Table 1): 12 of the 13 most frequent species in the 1980s were again among the most frequent 13 species in the 1990s. Of the 30 species analysed statistically, seven increased in frequency significantly (G_1>9.90, Dunn-Šidák corrected P<0.05), with the largest increase shown by the endemic Ashy-headed Laughingthrush *Garrulax cinereifrons*. Three species decreased in frequency significantly: Bar-winged Flycatcher-shrike *Hemipus pictatus*, Sri Lanka White-eye *Zosterops ceylonensis* and Yellow-fronted Barbet *Megalaima flavifrons*.

Flocks were also stable in their size and composition seasonally. For the 1996 and 1997–1998 surveys, the month of the observation did not affect the number of species in flocks ($F_{11,157}$=0.96, P>0.40), even though monthly rainfall varied five-fold, with a distinct dry season during January–March (Fig. 1). Migrants formed a minor component of flocks, with eight migrant species occurring in flocks but only one, Asian Paradise-flycatcher *Terpsiphone paradisi*, being a regular flock member during the months it was present. Only two species showed a strong difference in frequency between the dry (January–March) and wet seasons (April–December), consistent in both the 1980s and the 1990s (Table 1). These were Asian Paradise-flycatcher (1980s: G_1=36.8, P<0.001; 1990s: G_1=73.9, P<0.001), which was more frequent in the dry season, and Layard's Parakeet *Psittacula calthropae* (1980s: G_1=18.0, P<0.001; 1990s: G_1=10.2, P<0.001), which was more frequent in the wet season.

Foraging by flock members

While insectivores dominated flocks, omnivores and even frugivores joined flocks (Fig. 2; Table 1). Considering these three groups, diet had a significant effect on propensity ($F_{2,32}$=6.40, P<0.005, R^2=0.29), although only one of the three multiple comparisons, insectivores vs. frugivores, was significant (Gabriel multiple comparisons, P<0.05). Some omnivores may be largely insectivorous while in flocks: two species

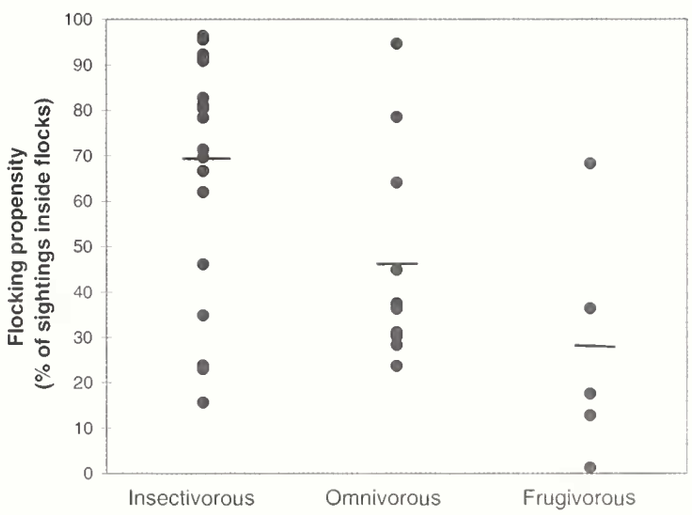

Figure 2. Insectivores had a higher flocking propensity (% individuals observed that were in flocks) than omnivores and frugivores. Points represent species that were observed at least 20 times. Lines represent means.

Table 1. Regular participants in mixed-species flocks in observations made in 1981–1998. Species are listed in order of their frequency in flocks in the total dataset (n=476).

Species[a]	Mean no. individuals/ flock[b]	% flocks in 1980s (n=219)	% flocks in 1990s (n=257)	% flocks in dry season (n=100)	% flocks in wet season (n=376)	Diet[c]	Foraging technique[d]	Flocking propensity[e]
ORANGE-BILLED BABBLER* *Turdoides rufescens*	16.2 (n=268)	91	92	99	89	If	LG (n=97)	92 (n=2440)
GREATER RACKET-TAILED DRONGO *Dicrurus paradiseus*	2.7 (n=316)	89	88	91	88	In	HA/ho (n=53)	92 (n=395)
MALABAR TROGON *Harpactes fasciatus*	1.9 (n=222)	53	68	63	61	If	HO/ha (n=43)	96 (n=205)
YELLOW-BROWED BULBUL *Iole indica*	2.3 (n=185)	47	58	50	53	IF		36 (n=433)
BLACK-NAPED MONARCH *Hypothymis azurea*	1.5 (n=178)	38	57	35	52	I	HA/ho (n=19)	67 (n=192)
RED-FACED MALKOHA*+ *Phaenicophaeus pyrrhocephalus*	2.2 (n=173)	42	54	40	51	IF	LG (n=29)	95 (n=151)
YELLOW-FRONTED BARBET* *Megalaima flavifrons*	2.0 (n=181)	57	41	51	47	Fa		68 (n=157)
SCARLET MINIVET *Pericrocotus flammeus*	2.8 (n=167)	42	53	26	54	I	ho/lg (n=17)	62 (n=306)
ASHY-HEADED LAUGHINGTHRUSH*+ *Garrulax cinereifrons*	7.2 (n=147)	33	59	28	52	If	LG/s (n=60)	91 (n=604)
DARK-FRONTED BABBLER *Rhopocichla atriceps*	3.3 (n=139)	33	54	30	48	I	LG (n=22)	35 (n=571)
INDIAN SCIMITAR BABBLER *Pomatorhinus horsfieldii*	1.8 (n=146)	38	50	39	46	Ifn	lg/wg (n=36)	71 (n=161)
LESSER YELLOWNAPE *Picus chlorolophus*	1.5 (n=143)	40	42	32	44	I	WT (n=29)	92 (n=86)
WHITE-FACED STARLING*+ *Sturnus albofrontatus*	2.7 (n=152)	41	38	46	38	IFn	LG (n=30)	79 (n=187)
SRI LANKA WHITE-EYE* *Zosterops ceylonensis*	7.3 (n=109)	38	21	19	31	IFN		64 (n=145)
VELVET-FRONTED NUTHATCH *Sitta frontalis*	2.7 (n=106)	26	30	29	28	I	WG (n=18)	81 (n=132)
BLACK-CRESTED BULBUL *Pycnonotus melanicterus*	2.0 (n=89)	19	35	17	31	IF		30 (n=252)
LAYARD'S PARAKEET* *Psittacula calthropae*	5.2 (n=80)	20	32	7	32	FN		36 (n=374)
PALE-BILLED FLOWERPECKER *Dicaeum erythrorynchos*	1.8 (n=90)	15	35	9	30	IFN		28 (n=205)
LEGGE'S FLOWERPECKER* *Dicaeum vincens*	2.0 (n=91)	19	32	14	29	IFN		45 (n=138)
BLACK BULBUL *Hypsipetes leucocephalus*	2.5 (n=73)	21	28	30	24	IFn		37 (n=185)
PALM SQUIRREL *Funambulus* sp.	1.2 (n=92)	22	28	23	26	IF		90 (n=58)
ASIAN PARADISE-FLYCATCHER *Terpsiphone paradisi*	1.3 (n=53)	14	9	38	4	I	HA/ho (n=41)	78 (n=51)

[a] * = endemic to Sri Lanka; + = Vulnerable (BirdLife International 2001).

[b] Figures in parentheses represent the number of flocks that had complete information on the number of individuals of the species.

[c] F = frugivorous, I = insectivorous, O = omnivorous. Upper case letters indicate the category is the principal food source, lower case letters indicate that the category is a minor part of the diet.

[d] Foraging technique of insectivorous birds: HA = hawking (no contact with substrate), HO = hovering (contact with bill on substrate), LG = leaf-gleaning, S = scratching on the ground, WG = wood-gleaning (where wood is the combination of trunks, branches and twigs), WT = wood-tapping (repeated probing). Upper case letters indicate that more than 50% of the foraging observations fit the category, lower case letters indicate that between 25% and 50% of the observations fit the category.

[e] % individuals seen in flocks out of all observations of species (Thiollay and Jullien 1998). Numbers in parentheses represent the total number of observations of that species, inside or outside of flocks, in the 1990s survey.

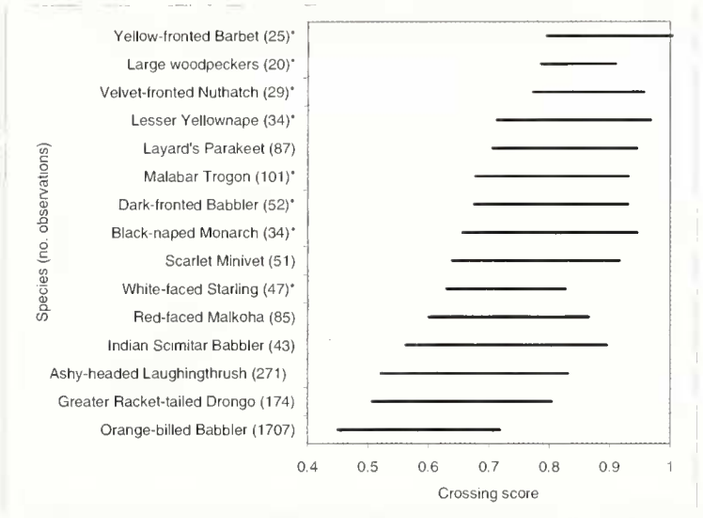

Figure 3. Horizontal organisation of flocks. For each species, lines represent the mean plus the standard deviation of the crossing score (the position of the bird in the crossing divided by the total number of birds that crossed). In order to show the relative dispersion of species in crossings, the standard deviation was calculated from the records of all individuals (shown in parentheses); in the statistical analysis, however, we averaged the records of individuals of a species for each of the 83 flock crossings. Species that had a crossing score that was significantly different to the score for Orange-billed Babbler are marked *. Large woodpeckers included both Greater Flameback *Chrysocolaptes lucidus* and Black-rumped Flameback *Dinopium benghalense*.

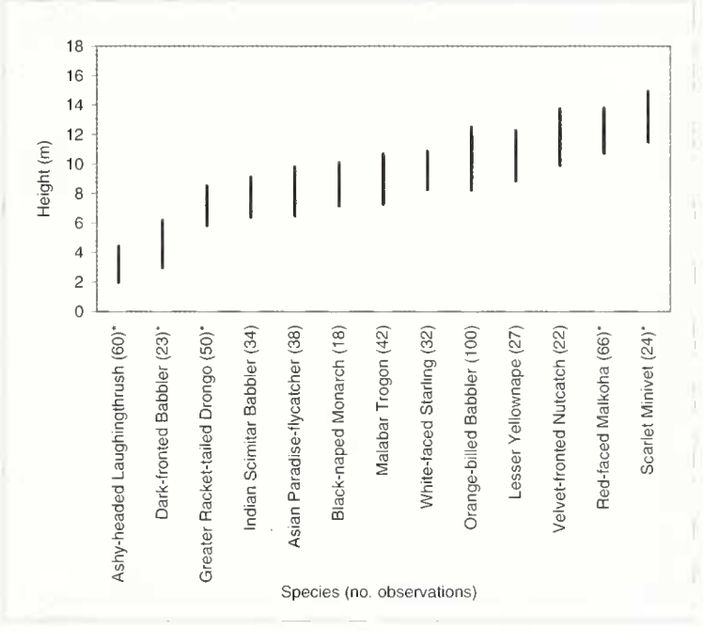

Figure 4. Vertical organisation of flocks. For each species, lines represent the mean plus the standard deviation of the species's foraging height. Species that foraged at heights that were significantly different to the height for Orange-billed Babbler are marked *.

Table 2. Flock leaders during road crossings. Only species that led flocks >3 times are listed. Sample sizes refer to number of flocks containing the species.

Species	% occasions led	% individuals in crossings
Orange-billed Babbler	72 (n=75)	60.2
Greater Racket-tailed Drongo	14 (n=64)	6.8
Ashy-headed Laughingthrush	21 (n=33)	17.4
Red-faced Malkoha	10 (n=31)	5.5

described in the literature as omnivorous, Red-faced Malkoha *Phaenicophaeus pyrrhocephalus* and White-faced Starling *Sturnus albofrontatus*, were seen to feed only on insects in flocks. Significant frugivore flock members included Yellow-fronted Barbet (common throughout the year) and Layard's Parakeet (regular between April and September).

Among insectivores, there was a wide range of foraging techniques in flocks (Table 1). Among the common species for which we had adequate sample sizes, we were able to characterise five species as primarily leaf-gleaning (Ashy-headed Laughingthrush, Dark-fronted Babbler *Rhopocichla atriceps*, Orange-billed Babbler, Red-faced Malkoha, and White-faced Starling), four species as hawking or hovering (Asian Paradise-flycatcher, Black-naped Monarch *Hypothymis azurea*, Greater Racket-tailed Drongo and Malabar Trogon *Harpactes fasciatus*), and two species as wood-probing or gleaning (Lesser Yellownape *Picus chlorolophus* and Velvet-fronted Nuthatch *Sitta frontalis*). Two other species (Scarlet Minivet *Pericrocotus flammeus* and Indian Scimitar Babbler *Pomatorhinus horsfieldii*) were difficult to characterise as they did not engage in one foraging technique or location in more than 50% of observations.

Spatial organisation of flocks

Orange-billed Babbler was the primary flock-leading species. Individuals of this species were the first birds to cross in the majority of road crossings (54 of the 75 crossings by flocks in which they were members), more than would be expected from their frequency in flocks (Table 3; G_1=4.55, P<0.033). Greater Racket-tailed Drongos led flocks much less often, although also more than would be expected by chance (G_1=4.08, P<0.044). Species varied significantly in their crossing scores ($F_{14,391}$=6.26, P<0.0001), with eight species being significantly behind babblers (Fig. 3; Tukey HSD multiple comparisons, P<0.05). The last species to cross included four wood-probing or gleaning species (Velvet-fronted Nuthatch, Lesser Yellownape, Greater Flameback *Chrysocolaptes lucidus* and Black-rumped Flameback *Dinopium benghalense*) and a frugivore (Yellow-fronted Barbet).

Flocks foraged from the ground to the canopy (although observations of the canopy were limited by the density of the vegetation and may be under-represented in the data). While species varied significantly in their foraging height ($F_{12,591}$=28.76, P<0.0001), most (7/12) foraged at heights statistically indistinguishable from Orange-billed Babbler (Fig. 4; Tukey HSD

Table 3. Nearest neighbours in flocks, and proximity to Orange-billed Babblers. *=distance is significantly greater than mean distance of Orange-billed Babblers to conspecifics.

Species	% cases closest to conspecific	% cases closest to babbler	Distance to nearest babbler	No. observations
Gregarious babblers				
Orange-billed Babbler	84	84	3.6 (±2.5)	82
Ashy-headed Laughingthrush	74	16	11.1 (±6.2)*	50
Dark-fronted Babbler	43	19	11.5 (±8.0)*	21
Non-gregarious babblers and other leaf-gleaning species				
Indian Scimitar Babbler	3	58	7.1 (±3.7)*	31
Red-faced Malkoha	18	66	6.8 (±4.8)*	62
White-faced Starling	14	73	4.7 (±3.4)	34
Woodpeckers				
Lesser Yellownape	7	62	7.8 (±4.4)*	29
Hawking or hovering species				
Asian Paradise-flycatcher	0	64	6.8 (±5.8)*	42
Black-naped Monarch	0	72	6.6 (±5.3)	18
Greater Racket-tailed Drongo	12	67	5.8 (±4.0)	43
Malabar Trogon	4	55	6.0 (±3.4)	41
Small canopy species				
Scarlet Minivet	24	32	10.8 (±7.5)*	25
Velvet-fronted Nuthatch	15	30	12.4 (±4.8)*	18

multiple comparisons, $P<0.05$). This result is unsurprising because babblers had the widest range of foraging heights of any species.

For seven of 12 species analysed, a majority of individuals were closest to an Orange-billed Babbler (Table 3). These species, especially those that hawk or hover for their prey, were rarely next to conspecifics. In contrast, small canopy species, and two gregarious members of the babbler family, were close to conspecifics and far from Orange-billed Babblers. Statistical tests are difficult to apply to the analysis of these data, since the exact percentage of Orange-billed Babblers in the flock at any one time is unknown: it is probably above 37% (the percentage of babblers in flocks) but below 60% (the percentage of babblers in road crossing observations, when birds in the periphery of the flock may have been uncounted). However, it is clear that the Ashy-headed Laughingthrush was found closest to babblers less often than would be expected by chance (8 of 50 observations; $G_1=11.1$, $P<0.0008$, assuming babblers form 37% of individuals in the flock), and Orange-billed Babblers were their own closest neighbours more often than would be expected by chance (81 of 97 observations; $G_1=24.7$, $P<0.0001$, assuming they form 60% of individuals).

DISCUSSION

Flocks in the Sinharaja lowland rainforest are distinct from flocks described from other regions of Sri Lanka, being larger and with a different species composition. They have a higher species diversity, containing many endemic and threatened species: 18 species (including eight regular members) were endemic to Sri Lanka (out of a total of 23 endemic species: Grimmett *et al.* 1999), and six species (including three regular members) are listed as Vulnerable (BirdLife International 2001).

While the flock system was generally stable between the 1980s and the 1990s, changes in the frequency of several species may relate to forest regeneration following logging in the 1970s. For example, Ashy-headed Laughingthrush, an endemic species that forages near the ground, increased in frequency by 26%, perhaps as a result of the development of a more mature and less dense understorey. The species that decreased the most—Bar-winged Flycatcher-shrike (-19%), Sri Lankan White-eye (-17%), and Yellow-fronted Barbet (-16%)—are often associated with large clearings and human-disturbed habitats, and such clearings were much reduced in size by the 1990s. These changes in flock composition suggest that flocks can be used to monitor environmental change. Future studies addressing how flock composition varies with the size and disturbance history of forest patches in the region would be valuable.

Comparison to flocks elsewhere

The Sinharaja flock system is distinct from that of the montane zone of Sri Lanka, although some species are present in both systems. Montane flocks always include Sri Lanka White-eye and/or Grey-headed Canary Flycatcher *Culicicapa ceylonensis* (Partridge and Ashcroft 1976). The latter species and two other frequent members of montane flocks—Great Tit *Parus major* and Yellow-eared Bulbul *Pycnonotus penicillatus*—are absent at the elevations of our study site in Sinharaja. Species shared by the two systems include Sri Lanka White-eye, Dark-fronted Babbler, Indian Scimitar Babbler, Velvet-fronted Nuthatch, and Dusky-striped Jungle Squirrel. Interestingly, Sri Lanka White-eye appeared to be an alternative nuclear species in Sinharaja, as 15 of the 20 flocks in which both the Orange-billed Babbler and the Greater

Racket-tailed Drongo were absent included white-eyes. Further studies should focus on investigating how flocks vary over an altitudinal gradient from lowland to montane.

Sinharaja flocks are typical of near-equatorial tropical flocks in that migrants form a small proportion of flock members, and that insectivores predominate over omnivores and frugivores. Migrants play a small role in flocks studied in the Neotropics (Munn and Terborgh 1979, Thiollay and Jullien, 1998), and in Malaysia and Borneo (McClure 1967, Laman 1992). In contrast, flocks in the Caribbean and southern Mexico include many migrant species (Hutto 1994, Latta and Wunderle 1996). Almost all flocks studied to date have a higher proportion of insectivores than frugivores. This is presumably because frugivores have patchily distributed food resources and thus do not move at a regular pace like many insectivores, and perhaps because the movement of the flock itself causes insects to flush (Powell 1985).

The flocks studied in Sinharaja are unusual, however, in their large size and the dominance of a single species. Comparing data from ten studies of flocks, the Sinharaja flocks ranked fourth out of ten in terms of number of species, and first in terms of numbers of individuals (McClure 1967, Laman 1992, Eguchi *et al.* 1993, Graves and Gotelli 1993, Hutto 1994, Latta and Wunderle 1996, Poulsen 1996, King and Rappole 2000, 2001a). The large flock size is a consequence of Orange-billed Babblers averaging more than 16 individuals per flock. Elsewhere, flocks usually include only a few individuals per species (Powell 1985).

Functions of flocking

The spatial arrangement of birds in flocks suggests that some species increase their foraging efficiency by associating with Orange-billed Babblers. Four species that foraged by hawking or hovering were closest on average to babblers. We believe it is likely that these species benefit from a 'beating effect' whereby they catch insects disturbed into the air by the leaf-gleaning babblers. We predict that further work will show that their foraging success is higher in flocks (cf. Hino 1998). Flock members may also benefit by copying the successful foraging behaviour of other species (Krebs 1973). Candidates for such benefits might include White-faced Starling and Red-faced Malkoha, omnivores that were only seen feeding on insects in flocks, usually close to babblers.

However, other groups of species, such as frugivores, wood-probing species and some of the gregarious babblers, are unlikely to increase their foraging in flocks. It is notable that frugivores and wood-probing species were usually at the back of the flock during road crossings, suggesting that the flocks may not have been travelling at these species' optimal foraging speed (Hutto 1988). Gregarious babblers such as the Ashy-headed Laughingthrush were usually next to conspecifics and thus would be unlikely to learn from heterospecifics. Species that do not benefit from foraging in flocks presumably benefit from reduced predation risk through a dilution effect (Terborgh 1990) and also by increased vigilance. Elsewhere we show that several flock species give alarm calls (Goodale and Kotagama in press).

Nuclear species

The Orange-billed Babbler is clearly a nuclear species for the Sinharaja flocks, i.e. it 'contributes appreciably to stimulate the formation and/or to maintain the cohesion of flocks' (Moynihan 1962). This species displays all the characteristics of nuclear species (Hutto 1994): they are present in most flocks, rarely seen away from them, highly gregarious, lead the flocks, and are constantly active and vocal. Congeneric species have been shown to live in closely related groups and to perform kin-selected behaviours that could be exploited by other species (Gaston 1977, Zahavi 1990).

Another potential nuclear species is Greater Racket-tailed Drongo, as this species is found in most flocks, it is rarely found outside flocks, leads the flock more than would be expected by chance, and is quite vocal. Drongos forage by flycatching, they are interspecifically aggressive (EG, personal observation), and have been reported to kleptoparasitise other species in mixed-species flocks (King and Rappole 2001b), so it is unlikely that other species gain any foraging benefits from associating with them. However, drongos give alarm calls that are more reliable than those of Orange-billed Babblers (Goodale and Kotagama in press), so other species may gain anti-predation benefits from joining drongos in flocks. Further behavioural observations may clarify the benefits that species gain from associating in flocks.

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REFERENCES

Ali, S., and Ripley, S. D. (1987) *Compact handbook of the birds of India and Pakistan, together with those of Bangladesh, Nepal, Bhutan and Sri Lanka.* Second edition. New Delhi: Oxford University Press.

BirdLife International (2001) *Threatened birds of Asia: the BirdLife International Red Data Book.* Cambridge, U.K.: BirdLife International.

De Zoysa, N., and Raheem, R. (1987) *Sinharaja, a rain forest in Sri Lanka*. Colombo: March for Conservation.

Eguchi, K., Yamagishi, S. and Randrianasolo, V. (1993) The composition and foraging behaviour of mixed-species flocks of forest-living birds in Madagascar. *Ibis* 135: 91–96.

Gaston, A. J. (1977) Social behaviour within groups of Jungle Babblers (*Turdoides striatus*). *Anim. Behav.* 25: 828–848.

Goodale, E. and Kotagama, S. W. (in press) Alarm calling in Sri Lankan mixed-species bird flocks. *Auk*.

Graves, G. R., and Gotelli, N. J. (1993). Assembly of avian mixed-species flocks in Amazonia. *Proc. Nat. Acad. Sci. USA* 90: 1388–1391.

Grimmett, R., Inskipp, C. and Inskipp, T. (1999) *A guide to the birds of India, Pakistan, Bangladesh, Bhutan, Sri Lanka and the Maldives*. Princeton: Princeton University Press.

Gunatilleke, C. V. S. and Gunatilleke, I. A. U. N. (1981) The floristic composition of Sinharaja rain forest in Sri Lanka, with special reference to endemics and dipterocarps. *Malay. Forest.* 144: 386–396.

Henry, G. M. (1971) *A guide to the birds of Ceylon*. Second edition. London: Oxford University Press.

Hino, T. (1998) Mutualistic and commensal organization of avian mixed-species foraging flocks in a forest of western Madagascar. *J. Avian Biol.* 29: 17–24.

Hutto, R. L. (1988) Foraging behaviour patterns suggest a possible cost associated with participation in mixed-species bird flocks. *Oikos* 51: 79–83.

Hutto, R. L. (1994) The composition and social organization of mixed-species flocks in a tropical deciduous forest in Western Mexico. *Condor* 96: 105–118.

King, D. I. and Rappole, J. H. (2000) Winter flocking of insectivorous birds in montane pine-oak forests in middle America. *Condor* 102: 664–672.

King, D. I. and Rappole, J. H. (2001a) Mixed species bird flocks in dipterocarp forest of north-central Burma (Myanmar). *Ibis* 143: 380–390.

King, D. I. and Rappole, J. H. (2001b) Kleptoparasitism of laughingthrushes by Greater Racket-tailed Drongos in Burma (Myanmar). *Forktail* 17: 121–122.

Krebs, J. R. (1973) Social learning and the significance of mixed-species flocks of chickadees (*Parus* spp.). *Canadian J. Zool.* 51: 1275–1288.

Laman, T. G. (1992) Composition of mixed-species foraging flocks in a Bornean rainforest. *Malayan Nature J.* 46: 131–144.

Latta, S. C. and Wunderle, J. M. (1996) The composition and foraging ecology of mixed-species flocks in pine forests of Hispaniola. *Condor* 98: 595–607.

Legge, W. V. (1880) *A history of the birds of Ceylon*. London: Self-published.

McClure, H. E. (1967) The composition of mixed-species flocks in lowland and sub-montane forests of Malaya. *Wilson Bull.* 79: 131–154.

Morse, D. H. (1977) Feeding behavior and predator avoidance in heterospecific groups. *BioSci.* 27: 332–339.

Moynihan, M. (1962) The organization and probable evolution of some mixed-species flocks of Neotropical birds. *Smithson. Misc. Coll.* 143: 1–140.

Munn, C. A. and Terborgh, J. W. (1979) Multi-species territoriality in Neotropical foraging flocks. *Condor* 81: 338–347.

Partridge, L. and Ashcroft, R. (1976) Mixed-species flocks of birds in hill forest in Ceylon. *Condor* 78: 449–453.

Phillips, W. W. A. (1935) *Manual of the mammals of Ceylon*. London: Dulau and Co.

Poulsen, B. O. (1996). Structure, dynamics, home range and activity pattern of mixed-species bird flocks in a montane alder-dominated secondary forest in Ecuador. *J. Trop. Ecol.* 12: 333–343.

Powell, G. V. N. (1985) Sociobiology and adaptive significance of interspecific foraging flocks in the Neotropics. *Ornithol. Monogr.* 36: 713–732.

Sokal, R. R. and Rohlf, F. J. (1995) *Biometry: the principles and practice of statistics in biologial research*. Third edition. New York: W. H. Freeman and Co.

Terborgh, J. (1990) Mixed flocks and polyspecific associations: costs and benefits of mixed groups to birds and monkeys. *Amer. J. Primatol.* 21: 87–100.

Thiollay, J.-M. (1999) Frequency of mixed-species flocking in tropical forest birds and correlates of predation risk: an intertropical comparison. *J. Avian Biol.* 30: 282–294.

Thiollay, J.-M. and Jullien, M. (1998) Flocking behaviour of foraging birds in a neotropical rain forest and the antipredator defence hypothesis. *Ibis* 140: 382–394.

Zahavi, A. (1990) Arabian Babblers: the quest for social status in a cooperative breeder. Pp. 105–130 in P. B. Stacey and W. D. Koenig, eds. *Cooperative breeding in birds: long-term studies of ecology and behavior*. Cambridge, U.K.: Cambridge University Press.

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